No. 10. — *The Rattle of the Rattlesnake.* By SAMUEL GARMAN.

THE habit of sloughing is common to all the serpents. A short time before the removal takes place, the new epiderm makes its appearance beneath the old. Its presence is easily detected by a whitish color under the outer layer. The milky tint of the second layer extends over the whole body; on the eyeball it interferes greatly with the sight. During the time of its formation, several weeks, while the vision is affected, the snake prefers seclusion, and is disinclined to partake of food. Some days before casting, about a week in the most recent case followed, the milkiness vanishes, the skin resumes its ordinary aspect, and the sight becomes again as keen as formerly. By rubbing the lips the slough is loosened around the mouth, then it is pushed over the head to the neck, whence it is taken back over the body. From the neck backward it is, in some cases, removed by means of a coil or two of the tail, the body being crowded through and the epiderm left behind. A hole in the ground or between rocks, the sticks in a brush heap or the stalks in the grass, answer the same purpose as the ring made by the tail. Some manage to get the coat back until under the ventral scales, when the latter are used somewhat as in gliding, their free hinder edges catching and stripping off the slough as the body is moved slowly forward. From the hinder part of the body the removal is an easier matter: the loosened portion is caught around a stick or under a stone, and with a pull the balance is taken off in an instant. The slough comes away like damp paper; it is wet with a sticky mucus on the inner side, turned outward in the operation. The mode of growth and of removal is similar among the rattlesnakes. These snakes differ in retaining a portion of each slough, that covering the tip of the tail, to form one of the rings of the rattle. The attachment is purely mechanical; the rings are merely the sloughs of the end of the tail.

On the majority of the snakes, both the venomous and the non-venomous, the tail tapers more or less gradually to a point. At the end it is protected by a sub-conical cap of the epiderm. Under the latter lies the skin, and under it again the termination of the vertebral column, — a bone formed of vertebræ that have coalesced and changed their shape until the outlines of the mass nearly resemble those of the surface of the tip. This terminal bone is hard externally, and cellular within; it contains and protects the extremities of the cord and vessels of the column in the positions occupied by them in the embryo before the consolidation was effected. In the different species the number of vertebræ included in this bone varies considerably; sometimes, also, it is seen to vary in individuals of the same species. Before the appearance of the scale-like folds on the tail of the embryo, the skin of the extremity is smooth; afterward, on some, the tip takes on the semblance of being protected on the sides by scales, the distal portions of which have blended with the cap, while their bases have remained distinct, much as if the conical envelope were still undergoing process of enlargement. In such cases the line of demarcation between the scales and the cap is irregular and indistinct. This condition obtains in species of Tropidonotus, Eutænia, Nerodia, and allies. The line of separation is very decided and regular in Crotalus. As the tail develops more slowly, the scales do not appear on it until after they are well formed on the body. Up to the time of their formation, the story of the caudal development of the rattlesnake is the same as that of any other serpent. The general shapes and the numbers of vertebræ differ greatly in the various kinds, but the history is similar in all. With the purpose of indicating the manner of growth of the rattle, and, as far as may be, of determining its origin, we shall have to follow it up through different species, a complete series of any one of them not being at hand.

Sistrurus, Garm. Figs. 1–4.

Crotalophorus, Gray, not of Linné.

S. miliarius, Linn., is the only rattlesnake of which we have a good series of the very early embryos. Some of these, already three inches in length, are not yet furnished with scales on the tail, though the entire body is well provided. Outwardly, in these specimens, the tail is short, thick, blunt, slightly compressed, and has no indication of the characteristic feature so prominent after birth. The vertebræ are separate.

Figures 1 and 2 of the diagrams are drawn from embryos of *S. catenatus*, Raf. (*Crotalus tergeminus*, Say), six and a quarter inches in length. Their only promise of the rattle is to be noted in the shape and size of the cap, or button. Upon the body the scales are perfect; the button evidently is incomplete, being little more than half of what it ultimately becomes. If a button as it is at birth were to be cut through the constriction immediately behind the anterior swelling, the hinder portion would correspond with the cap as seen in Figures 1 and 2. There is no evidence of any fusion of scales with the button around its front border. Except in case of the button, there is externally very little difference between this stage and the next represented. Within the cap the vertebræ are distinct, slightly smaller than those just in front of them, like the latter surrounded by muscles, and the skin is thicker than elsewhere. Between this stage and the following the anterior portion of the cap appears to be added by backward growth at the front margin, like that which later in life displaces the older button to make way for the new.

Figures 3 and 4 are drawn from young ones of the same species, *S. catenatus*, Raf., eight and a quarter inches in length, about a week after birth. In them the button has been perfected, the cap having gained, as compared with Fig. 2, all the portion anterior to the constriction. On several of these specimens there is a tendency to fusion and irregularity among the scales immediately in front of the button, but in no case is there any disposition on the part of the scales to fuse with the latter. A portion of the button corresponding to the externally visible part of each ring has been acquired, while the entire length has increased a couple of inches, in a short time just before birth. Inside of the button the changes have been greater: the vertebræ, still plainly outlined, have consolidated into a single elongate mass, the size of which is being increased by both lateral and terminal growth; the vertical processes have grown together; and the muscles have been displaced by the enlarging bone and the thickening skin. Muscular command of the individual vertebræ within the button has been lost in the consolidation, but the muscles of the tail retain a firm hold on the mass, and the loss finds compensation in a better means of agitating the rattle. For later stages we are compelled to turn to a closely allied genus.

Crotalus, Linné.

Crotalophorus, Linn.; *Caudisona*, Laur.

Figures 5 and 6, from a *Crotalus confluentus*, Say, fourteen inches in length, show a considerable advance from the preceding. The specimen was taken, with the third button about half grown, when the process of pushing back the second ring was well under way. The first ring had been set free with the first slough, holding only by the collar; and if the snake had been allowed to live a little longer, the second sloughing would have discovered the third button perfected, clasped by the second ring, the latter pushed back and loosened from the balance of the epiderm. Of the second ring the narrower posterior extension is quite empty; its anterior chambers are closely filled with the tumid skin, the loss of the ring being prevented in this manner, while the outer swelling of the new button is crowding it backward. A considerable shrinkage of the skin takes place after the moult; it is insufficient to allow the ring to slip off, though admitting of great freedom of motion. In front of the border of the second ring, Fig. 5, lies the fold, shrunken by alcohol in the specimen, by which the ring was displaced, and which was to become the largest chamber of the next succeeding. This fold is usually hidden by the epiderm attached to the ring, as in Fig. 6, until the operation of sloughing has been finished. The mass of bone occupies the place of eight or more of the vertebræ in this stage, the lines of separation being still noticeable to some extent. By a longitudinal section the cord and vessels are disclosed in their original positions, surrounded now by spongy bone, in which the cavities radiate from the centre toward the surfaces. On the upper and lower faces there is less indication of the composition.

Figures 7 and 8 were taken from a large specimen of *Crotalus horridus*, Linn. In it the traces of the vertebræ in the terminal bone are almost obliterated; the bone has thickened, pushed forward at the edges, and otherwise enlarged. Along with this there has been an excessive development of the muscles of the tail. The rattle is entire, of eleven rings and a button. The hinder seven of the rings belong to the period of the snake's most rapid growth; they form the "tapering rattle" common to the young individuals, formerly used in classification of the species by some authors. Four of the rings and the button pertain to a part of the creature's life in which the gain in size was much less rapid; they form the "parallelogramic rattle" of the same writers. The mistaken use of these features in specific diagnoses no doubt arose from study of incomplete rattles. The change from the taper to the more nearly parallelogramic takes place about the seventh ring, — in *Sistrurus miliarius* often with the sixth, with the larger species frequently with the eighth, — and affords the means of obtaining an approximate idea of the comparative age of the owner of the series of rings. The figures show the rattle as commonly held by the snake when crawling. In a single series of rings there is much variation in shapes, as in sizes, and there are also considerable differences in the rattles within the species. In the case of the small snake *Crotalus exsul*, Garm., from Cedros Island, Lower California, the large size of the first ring is evidence of derivation from a larger species, probably *C. lucifer*, B. & G., of the mainland. In this case, the change in button has not kept pace with the reduction in size of body, or the changes in squamation, etc. While the rings vary with rapidity of growth in the body, from amount of food, it is unlikely that it makes an, difference in their number, or that of the sloughings.

More than seventy specimens have been looked over for evidence of growth of a new button between the months of May and September; two, and a doubtful third, favor the conclusion that a ring is added in the fall. One of these, as it was in September, is sketched in Figures 5 and 6. On the other hand, living specimens kept through the winter prove that a new growth does take place toward spring, and that when the epiderm is shed, on coming out of winter quarters, the animal is possessed of an addition to the rattle.

The mechanism of the organ has been so often described and figured that it is unnecessary to give a detailed description here. Among the most accurate of the earlier writers is Lacépède, 1789 (Histoire des Serpens, II. pp. 390–420, Pl. XVIII.); and of the more recent, Czermak, 1857 (Ueber den schallerzeugenden Apparat von Crotalus, in Vol. XIII. of the Zeitschrift für wissenschaftliche Zoologie, pp. 294–302, Pl. XII.). For comparison with what has been recorded above, a few sentences are quoted from Lacépède (p. 404). Speaking of the mode of growth, he says: "Quand une pièce est formée, il se produit au-dessous une nouvelle pièce entièrement semblable à l'ancienne, et qui tend à la détacher de l'extrémité de la queue. L'ancienne pièce ne se sépare pas cependant tout-à-fait du corps du serpent; elle est seulement repoussée en arrière; elle laisse entre son bord et la peau de la queue, un intervalle occupé par le premier bourlet de la nouvelle pièce; mais elle enveloppe toujours le second et le troisième bourlets de cette nouvelle pièce, et elle joue librement autour de ces bourlets qui la retiennent. . . . Si les dernières vertèbres de la queue n'ont pas grossi pendent que la sonnette s'est formée, chaque pièce qui s'est moulée sur ces vertèbres a le même diamètre; et la sonnette paroit d'une égale largeur jusqu'à la pièce qui la termine; si, au contraire, les vertèbres ont pris de l'accroissement pendant la formation de la sonnette, les bourlets de la nouvelle pièce sont plus grands que ceux de la pièce plus ancienne, et le diametre de la sonnette diminue vers la pointe."

The anatomy of Crotalus was studied by Tyson in 1683 (Philosophical Transactions, No. 144).

In regard to the use of the rattle there is not much to be said. Mainly, it is used to warn off disturbers, and thus prevent useless expenditure of venom. Success in capture of food depends on an ever ready supply of poison. To secrete a new lot takes time. The rattle is used also in breeding season, though it is doubtful if the dull-eared creatures depend on sound, rather than scent, to find their mates. A theory advocated by some maintains that the organ is used in imitating insects, to draw the birds. An objection to this is the fact that birds are somewhat rarely found in stomachs of the Crotali. An observation appearing to favor this theory was made on a Dakota snake, found braced up among the branches of a sage bush in such a way that the head overlooked the surrounding bushes, while the tail, within the mass of branchlets, was free to keep up the rattling that attracted the attention of a party more than fifty yards distant. But the approach of the troop may have occasioned the creature's peculiar behavior.

Origin of the Rattle.

Many serpents besides those possessed of a crepitaculum are addicted to making a rattling noise by vibrations of the end of the tail. It is likely the modifications of the organ apparent in some or others of these are consequences of this habit. In illustration of the extent to which the tail has been modified in different cases, apparently for similar purpose, attention is directed to Figures 9–14, from species allied to the rattlesnakes.

Rhinocerophis ammodytoides, Leybold, Figs. 9, 10, from the Argentine Confederation, has its most prominent distinguishing features in a prominence on the top of the snout, and, of more importance in this writing, a peculiar termination of the tail. Fig. 9 outlines the caudal surface. The terminal piece is sub-crescentic in longitudinal vertical section, and sub-round in transverse. Externally it is covered by the horny skin, internally it is bony. On the top, two of the dorsal scales reach back more than a third of the length, and near their tips fuse with each other and the skin about them. Fig. 10 shows the arrangement after the skin and muscles have been removed. The outside of the bone is hard, the inside not solid. It is penetrated by the canals of the vertebræ, — indications of its origin. Inferiorly, it extends forward below three of the vertebræ, firmly anchylosed to it and to each other, the anterior of the three being partly subtended. In front of it, the column is normal. Each vertebra is long, low, rather broad, and vertically crossed in the middle by a light line, as if two had joined end to end. The neural spines are low, inclined backward, and, in the hinder three or four, expanded laterally on the upper edge into a flange that in the posterior unites with the terminal bone. Zygapophyses and parapophyses are feebly developed; the hypapophyses are blade-like, thin, and fragile. Appearances suggest that the tip is carried upon and struck against the ground.

On *Lachesis mutus*, Linn., Fig. 11, from Brazil and Northern South America, the end of the tail is a long, slender, compressed, cultriform blade. The scales in front of it are small and tubercular. This is especially the case with a dozen or more of the sub-caudals, that, as they approach the end, are subdivided and spine-like. Within the cap the bone is similar to those described above. The vertebræ preceding it are slender, with weak processes. Near the extremity the tail is slender and very flexible, a condition enhanced by the smallness of the scales. It looks as if it were carried off the surface.

Halys acutus, Gth., Fig. 12, is a serpent recently described by Dr. Gunther, 1888 (Ann. Mag. Nat. Hist., (6), I. 171, Pl. XII.), from the mountains north of Kiu Kiang, China. It is remarkable on account of a flexible pointed lobe extended from the end of the snout, and for the peculiar scutellation of its compressed tail. Dr. Gunther says the tail is not to be in any way taken as an initial step in the development of the rattle of Crotalus, though the organ in this species may in a much smaller degree exercise the same function as in the rattlesnake, being an instrument by which vibrations and sound are produced. From what we have seen above, it is not difficult to imagine a rattle developed from the arrangement of scales and vertebræ present in this snake. However, as Dr. Gunther remarks, and as illustrated below, it is quite unnecessary to suppose the tail of Crotalus has gone through such modification.

Ancistrodon piscivorus, Holbr., Fig. 13, the Moccasin, from the Southern United States, is similar to Rhinocerophis in the structure of the tip. The terminal bone is not so greatly developed. A greater number of scales have fused with the cap.

On *Ancistrodon contortrix*, Linn., Fig. 14, the Copperhead, of the United States to Mexico, the tip differs a little from that of its congener, the Moccasin; it is directed downward as well as backward. Most often the cap, or button, has one or two swellings in a degree resembling those on a ring of the rattle. A living specimen of this snake, kept for a year or more, would take to rattling on the floor whenever he was irritated. The sound was made by the terminal inch of the tail, this part being swung from side to side in the segment of a circle, so that the tip might strike downward. The result was a tolerable imitation of that made by a small rattlesnake.

Both Copperhead and Moccasin bear evidence of union between cap and scales. All the specimens have two scales fused above and two below the button; some show that more have joined the two above, and that one or more of the laterals has been included on the sides.

The testimony of the embryo is to the effect that the rattlesnakes were derived from forms in which the terminal vertebræ were not fused into a terminal bone. There seems to be no radical difference, in the earlier stages of the end of the tail, between the above mentioned as well as other non-crotalophorus forms and Crotalus. So much divergence in the number and shape of the caudal vertebræ occurs in the various genera, that these features become matters of secondary interest in a general comparison. In the later development the rattlesnake goes farther than any of the others. The bone at the end of the column is of the same nature throughout the Ophidia. On Crotalus it eventually contains a greater number of vertebræ, there is a greater enlargement of the mass, and in devoting it exclusively to shaking the rattle, instead of striking upon objects, a different use is made of it. In front of the rattle the neural spines incline forward, possibly a consequence of the function of the tail. This inclination has little weight when compared with forms like Ancistrodon, where the spine is so low. Similar leaning toward the head occurs in the Hydrophidæ and in Ogmophis, a Tertiary fossil of uncertain affinity. So far as the vertebræ are concerned, they point to no special one of the recent allies as representative of the stock from which the rattlesnakes have sprung.

With the button there is but little more success. While it might possibly have been formed or enlarged by fusion of scales with the cap, there is really no reason to suppose scales were formed on the end of the tail only to be lost again. In fact, embryonic data favor the conclusion that it was formed by simple enlargement, or expansion of the cap itself. A cap that by its shape would be mechanically held to its successor might be produced by slight changes in that of any one of a number of species of the family, in addition to those figured. Shape is the important feature in the retention of the series of caps. This, in the rattlers, is obtained through that of the end bone, the thick skin covering the latter, and the mode of growth. Generally, on the pointed tip there is no chance to retain the cap during and after the slough. Without the backward growth from the front border at the time of forming the cap, again, the rattle would not exist, as each new cap would be formed entirely within its predecessor. *Ancistrodon contortrix*, the Copperhead, Fig. 14, gives a hint of the probable manner of origin of the rattle, in the folds, or swellings, at the front border of the cap. The presence of these folds apparently indicates that growth from the margin has taken place. If, as seems to be the case from the folds, the necessary manner of growing already exists, but a slight increase in it, increasing the amount of the swellings and constrictions, would be needed to provide the Copperhead with a rattle. After the retention of the displaced cap was secured, the change from the habit of striking the tip upon the ground to simple shaking would be followed by loss of flexibility in the tail itself, by rigidity of the column, — a condition, with inclusion in the cap and the peculiar strain on the muscles, favoring consolidation of the terminal vertebræ, and tending to draw the spines forward. It appears very much as if the rattle originated in some such way.

Though the Copperhead has been specially used as an illustration here, it is not asserted that the rattlesnakes are directly derived from it. Taking the general characteristics into consideration, it seems more likely they took origin in several stocks; one of them, allied rather closely to Ancistrodon, yielding the Sistruri (the small rattlesnakes with large crown shields); another, nearer to Lachesis, giving rise to *Crotalus durissus* and allies.

In summarizing, we may say the rattlesnakes have probably been derived from members of the same family that had no rattle. The button of the rattle was formed by enlargement of the terminal cap covering the terminal bone, very likely without fusion with scales. The shape of the button was determined by that of the bone and skin of the tip; it is modified in the second and following rings by the ring immediately preceding. The exterior or exposed part of each button after the first, is formed in front of the ring with which it is in contact, and pushes the latter back. As the button is displaced to become a ring, it is prevented from passing entirely off by the swollen skin, completely filling its anterior chambers, behind the constrictions. The development of the button and the rattle was accompanied by a consolidation and compacting of a larger number of the vertebræ, with loss of the muscles directly belonging to the reduced portion, and with greater development of the muscles in front of it. And, finally, the probability that the rattlesnakes represent at least two lines of descent may be added; one, that of Sistrurus, more closely connected with the Copperheads; another, that of *Crotalus durissus* and allies, connecting with that of *Lachesis mutus.*

April 16, 1888.

LIST OF DIAGRAMS.

PLATE I.

PLATE II